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The first International Conference on the Systematics of the Euphorbiaceae was held at the Missouri Botanical Garden in St. Louis on 14–16 August 1989. Papers were presented by 21 people (several of these with one or more collaborators); of these, 15 authors submitted papers that were accepted for publication and are presented in this issue and the one preceding.

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# THE CONTRIBUTION OF EMBRYOLOGY TO THE SYSTEMATICS OF THE EUPHORBIACEAE<sup>1</sup>

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## ABSTRACT

The Euphorbiaceae are often described as a heterogeneous group with ambiguous affinities. Although their vegetative and floral characters are markedly modified in relation to the habitat and pollination mechanisms, the embryological features are comparatively more conservative, and therefore quite useful in the delimitation of as well as in understanding of relationships. The diagnostic embryological characteristics of the family are: (1) tetrasporangiate anther, 4- or 5-layered anther wall, fibrous endothecium, ephemeral middle layer(s), secretory tapetum with multinucleate cells, simultaneous cytokinesis, tetrahedral, decussate and isobilateral microspore tetrads, and 2- or 3-nucleate pollen; (2) tricarpellary, syncarpous, and trilocular ovary with one or two ovules in each locule, axile placentation, anatropous or hemianatropous, bitegmic, crassinucellate ovule, placental obturator and presence of hypostase; (3) embryo sac with ephemeral antipodal cells, nuclear endosperm and mature embryo with broad/leafy cotyledons; and (4) albuminous seed with both integuments forming seed coat, and outer epidermis of inner integument developing into a fibrous or sclerotic layer. Most of the 30 families included in the Euphorbiales by various authors have significant embryological differences from Euphorbiaceae. It appears more appropriate that the Euphorbiales should include only one family, the Euphorbiaceae. The closeness of the Euphorbiales with the Malvales finds support on embryological grounds. The present level of embryological information substantiates the classification of the Euphorbiaceae into five subfamilies. It seems that the Acalyphoideae diverged rather early from the Phyllanthoideae-Oldfieldioideae, and later the Crotonoideae and the Euphorbioideae evolved as independent lines from the Acalyphoideae. Since only 16 of the 50 tribes have so far been embryologically explored, comments on the tribal classification must await further probes into their reproductive biology.

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The Euphorbiaceae represent a large group of flowering plants distributed in almost all parts of the world, except the arctic regions. The family includes 300 genera and 8000 species (Webster, 1987a) predominantly distributed in the tropical and subtropical areas of both the New and Old Worlds. Because of the great variability in vegetative and floral characters, the group has been described as heterogeneous and highly diversified (Webster, 1967; Corner, 1976).

It is being increasingly realized that a natural or phylogenetic classification, be it of the angiosperms as a whole, or of a class, order, or family, cannot be based solely on morphological characters. The external features are often drastically modified in relation to environmental stress and fail to reflect true phyletic trends. Embryology has, therefore, acquired an important place, along with other disciplines such as cytology, anatomy, palynology, and chemotaxonomy, as a dependable tool in systematics. Embryological features are especially significant in situations where exomorphology either leads to inconclusive correlations or may even delude due to convergence (Kapil &

Bhatnagar, 1980). Wagenitz (1975) rightly emphasized that "for elucidation of the systematic position of groups with simple flowers embryological and phytochemical characters are especially valuable, as classical characters of flower may be too seriously altered by reduction." The embryological characters have also proved useful in: (i) determining the limits of a taxon, especially at the level of a family or order; (ii) ascertaining affinities when two or more possibilities are suspected; and (iii) evaluating a scheme of classification.

In the Euphorbiaceae, the sporophytic characters exhibit tremendous diversity. They help in recognizing natural groups down to the level of species and even below. On the other hand, the highly reduced gametophytic generations display much less variability. They are quite uniform at the generic level and above. They are more convincing not only in circumscribing the family, but also in judging its affiliations and in classifying it into subfamilies and tribes.

Considering the large size, the Euphorbiaceae are embryologically poorly known. Only 16 tribes (and about 30 genera), out of 50 tribes recognized

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by Webster (1987a; 1989, privately circulated), have been investigated. Some genera of economic importance, e.g., *Ricinus* L. and *Hevea* Aublet, and others of horticultural interest, e.g., *Acalypha* L., *Jatropha* L., and *Euphorbia* L., are well studied (see Table 1). It seems that the choice of the investigated species has depended on the availability of research material rather than on systematic considerations.

In the Phyllanthoideae, *Putranjiva* Wall., *Phyllanthus* L., *Breynia* J. R. & G. Forster, and *Bischofia* Blume are embryologically well known, whereas *Agyneia* L., *Meineckia* Baillon, *Sauropus* Blume, and *Securinega* Juss. are partially understood. The Oldfieldioideae are almost unknown except for some information on the ovule and seed of *Micranthemum* Desf. and *Androstachys* Prain, and the pollen and ovule of *Picrodendron* Planch. Subfamily Acalyphoideae, with 18 tribes, is familiar to the embryologist through studies on nine genera belonging to three tribes, viz. *Chrozophora* A. Juss. of Chrozophoreae, *Mallotus* Lour., *Mercurialis* L., *Ricinus*, *Micrococca* Benth., *Trewia* L., and *Acalypha* of Acalphyaeae, and *Tragia* L. and *Dalechampia* L. of Plukenetieae. In the Crotonoideae, which have been subdivided into 13 tribes by Webster (1987a; 1989, privately circulated), only seven genera belonging to six tribes have been explored. These are *Hevea*, *Manihot* Mill., *Jatropha*, *Codiaeum* A. Juss., *Croton* L., *Baliospermum* Blume, and *Aleurites* J. R. & G. Forster. In the Euphorbioideae, a disproportionately large body of embryological data are available for *Euphorbia*. The only other genera that have been investigated are *Sebastiania* Sprengel and to some extent *Sapium* P. Browne, *Excoecaria* L., and *Hura* L.

The paucity of embryological data can be partly ascribed to the difficulty in collecting a close series of developmental stages of buds, flowers, and fruits. The processing of material, sectioning, and staining are laborious and time-consuming procedures. In spite of these limitations, embryology has helped to solve some controversies (see Kapil & Bhatnagar, 1980). More and more taxonomists are taking embryological information into account when suggesting new schemes of classification and taxonomic relationships (see Dahlgren, 1975, 1980; Takhtajan, 1980; Cronquist, 1981; Thorne, 1983; Goldberg, 1986).

The main objective of this contribution is to document the ways in which embryology has contributed toward deciding the status of the Euphorbiaceae in the Euphorbiales, elucidating affinities of the Euphorbiaceae, and in determining how best this family can be classified into subfamilies.

#### EMBRYOLOGICAL CHARACTERS OF THE EUPHORBIACEAE

The following set of correlated embryological features (see Wunderlich, 1967; Kapil & Bhatnagar, 1972; Webster & Rupert, 1973) characterizes the Euphorbiaceae:

1. Tetrasporangiate anther, 4- or 5-layered anther wall, fibrous thickenings in endothecium, ephemeral middle layer(s), single layered tapetum of secretory type, bi- or multinucleate tapetal cells, often with lobed multinucleolate nuclei, simultaneous cytokinesis, tetrahedral, decussate or isobilateral microspore tetrads, 2- or 3-nucleate pollen grains.
2. Tricarpellary, syncarpous, trilocular ovary with two (Phyllanthoideae and Oldfieldioideae) or one (Acalyphoideae, Crotonoideae and Euphorbioideae) ovules in each locule, axile placentation, anatropous or hemianatropous, bitegmic, crassinucellate ovules, ventral raphe, funicular vascular supply terminating in chalaza or entering the base of nucellus or integuments, placental obturator, well-differentiated hypostase, hypodermal single or multicelled achesporium, female gametophyte with ephemeral antipodal cells, fusion of polar nuclei near egg apparatus.
3. Primary endosperm nucleus dividing earlier than zygote, nuclear endosperm, embryo with large/leafy cotyledons.
4. Seed with copious endosperm containing oil and starch, persistence of hypostase in the seed, formation of seed coat by both integuments, outer epidermis of inner integument differentiating into mechanical palisade or fibrous layer, and proliferative tip of outer integument often producing the caruncle.

#### DISTRIBUTION OF SOME EMBRYOLOGICAL CHARACTERS IN THE EUPHORBIACEAE

*1. Pollen nuclear number.* There is an interesting assortment of distribution of 2- and 3-nucleate pollen grains in the Euphorbiaceae. *Euphorbia* is one of the five exceptional angiosperm genera in which both 2- and 3-nucleate pollen grains occur in different species (Brewbaker, 1967; Webster & Rupert, 1973). In his study, which included 17 genera (35 species) of the Euphorbiaceae, Brewbaker (1967) observed that 13 genera had 2-nucleate pollen, 3 had 3-nucleate and only 1 had species with 2- or 3-nucleate pollen. Among 16 species of *Euphorbia* investigated, some species had 2-nucleate and others 3-nucleate pollen grains. He concluded that the distribution of 2- and

TABLE 1. Embryological studies in the Euphorbiaceae. +: presence; -: absence.

Genus (tribe)	Author(s)	An-ther	Ovule	Em-bryo sac	Endo-sperm	Em-bryo	Seed
Phyllanthoideae (11 tribes)							
<i>Putranjiva</i> Wallich (Drypeteae)	Dutt (1942); Banerji & Dutt (1944); R. P. Singh (1970a)	+	+	+	+	-	+
<i>Neopeltandra</i> Gamble (= <i>Meineckia</i> Bailon) (Phyllanthaceae)	P. N. Rao (1970); Venkateswarlu et al. (1973)	+	+	-	-	-	-
<i>Securinega</i> Juss. (Phyllanthaceae)	Bhatnagar & Kapil (unpublished); Corner (1976)	-	+	+	-	-	+
<i>Breynia</i> J. R. & G. Forster (Phyllanthaceae)	Thathachar (1953b); Venkateswarlu et al. (1973); Corner (1976)	+	+	+	+	+	+
<i>Melanthesa</i> Blume (= <i>Breynia</i> J. R. & G. Forster) (Phyllanthaceae)	R. P. Singh (1968)	-	+	-	+	+	+
<i>Agyneia</i> L. (= <i>Glochidion</i> J. R. & G. Forster) (Phyllanthaceae)	Mukherjee (1962); Corner (1976)	+	+	+	-	-	+
<i>Phyllanthus</i> L. (Phyllanthaceae)	R. P. Singh (1956, 1972); Dang-Van-Liem (1962); Mukherjee & Padhye (1964); Chopra & Singh (1969)	+	+	+	+	+	+
<i>Sauropus</i> Blume (Phyllanthaceae)	P. N. Rao (1970)	+	+	-	-	-	-
<i>Bischofia</i> Blume (Bischofiaceae)	Bhatnagar & Kapil (1973, 1979); Corner (1976)	+	+	+	+	+	+
Oldfieldioideae (3 tribes)							
<i>Androstachys</i> Prain (Picrodendreae)	Dahlgren & van Wyk (1988)	-	+	-	-	-	+
<i>Picrodendron</i> Planchon (Picrodendreae)	Hayden et al. (1984); Hakki (1985)	-	+	-	-	-	-
<i>Micrantheum</i> Desf. (Caletieae)	Berg (1975)	-	+	-	-	-	+
Acalyphoideae (18 tribes)							
<i>Chrozophora</i> A. Juss. (Chrozophoreae)	Kapil (1956a, b); Dang-Van-Liem (1962); Bor & Kapil (1976)	+	+	+	+	+	+
<i>Ricinus</i> L. (Acalypheae)	R. P. Singh (1954); Dang-Van-Liem (1962)	-	+	-	+	+	+
<i>Micrococca</i> Benthham (Acalypheae)	P. N. Rao (1962); Nair & Abraham (1963)	+	+	+	+	+	+
<i>Acalypha</i> L. (Acalypheae)	Tateishi (1927); Landes (1946); Thathachar (1952); Johri & Kapil (1953); Kapil (1960); Mukherjee (1958, 1964)	+	+	+	+	+	+
<i>Mercurialis</i> L. (Acalypheae)	Dang-Van-Liem (1962); Corner (1976)	-	-	-	-	+	+
<i>Mallotus</i> Loureiro (Acalypheae)	Ventura (1934); Thathachar (1953a); Raju & Rao (1953)	+	+	+	+	+	-
<i>Trewia</i> L. (Acalypheae)	Banerji & Dutt (1944)	-	+	+	-	-	-
<i>Tragia</i> L. (Plukenetieae)	Mukherjee (1962, 1968); Nair & Abraham (1980)	+	+	+	-	-	-
<i>Dalechampia</i> L. (Plukenetieae)	R. P. Singh & Pal (1968); G. L. Webster & B. D. Webster (1972)	-	+	+	+	+	+

TABLE 1. Continued.

Genus (tribe)	Author(s)	An-ther	Ovule	Em-bryo sac	Endo-sperm	Em-bryo	Seed
Crotonoideae (13 tribes)							
<i>Hevea</i> Aublet (Micrandreae)	Muzik (1954); Bouharmont (1962); A. N. Rao (1964)	-	+	+	+	+	+
<i>Manihot</i> Miller (Manihoteae)	P. N. Rao & Sarveswara Rao (1976); Dang-Van-Liem (1962); Corner (1976)	-	-	-	-	+	+
<i>Jatropha</i> L. (Jatropheae)	Mukherjee (1962); R. P. Singh (1970b)	+	+	+	-	-	+
<i>Baliospermum</i> Blume (Codiaeae)	P. N. Rao (1970)	+	+	-	-	-	-
<i>Codiaeum</i> A. Juss. (Codiaeae)	Galimberti (1963); R. P. Singh (1965); Bor & Bouman (1974)	-	+	+	+	-	+
<i>Croton</i> L. (Crotoneae)	Thathachar (1953b); Venkateswarlu & Rao (1963); R. P. Singh & Chopra (1970)	+	+	+	+	+	+
<i>Aleurites</i> J. R. & G. Forster (Aleuritidae)	Wiehr (1930); McCann (1945); Sharma (1955)	+	+	+	-	-	+
Euphorbioideae (5 tribes)							
<i>Excoecaria</i> L. (Hippomaneae)	P. N. Rao (1970)	+	+	-	-	-	-
<i>Sapium</i> P. Browne (Hippomaneae)	Chopra (1970); Corner (1976)	-	+	+	-	-	+
<i>Sebastiania</i> Sprengel (Hippomaneae)	Thathachar (1953b); Nair & Maitreyi (1962)	+	+	+	+	+	+
<i>Hura</i> L. (Hureae)	P. N. Rao (1970)	+	+	-	-	-	-
<i>Euphorbia</i> L. (Euphorbieae)	Kapil (1961); R. P. Singh & Jain (1965); R. P. Singh (1969); Bor & Kapil (1975); Battaglia (1986)	+	+	+	+	+	+

3-nucleate pollen within the Euphorbiaceae was random.

Webster & Rupert (1973) investigated 66 species belonging to 42 genera. They found a definite phylogenetic pattern in the distribution of 2- and 3-nucleate pollen. For example, the biovulate subfamilies Phyllanthoideae and Oldfieldioideae had 2-nucleate pollen in 14 genera. Among the uniovulate subfamilies, the Acalyphoideae showed the 2-nucleate condition. In the Crotonoideae, 2-nucleate pollen grains are found in a larger number of tribes (Jatropheae, Gelonieae, Codiaeae, Ricinocarpeae, Aleuritidae, Neoboutoniae) and 3-nucleate in fewer (Micrandreae, Manihoteae, Crotoneae). In the Euphorbioideae (sensu Webster, 1987a) both the large tribes Hippomaneae and Euphorbieae have 2- and 3-nucleate genera (Webster et al., 1982).

In angiosperms, the 2-nucleate condition of pollen is considered primitive and 3-nucleate advanced. The shift from the 2-nucleate to 3-nucleate condition is regarded as irreversible (Webster & Rupert, 1973; Goldberg, 1986). It therefore seems

that in the Euphorbiaceae the 3-nucleate condition has evolved independently, perhaps more than once, in the Crotonoideae and Euphorbioideae.

2. *Integument initiation in the ovule.* Carpellary and ovular characteristics in the Euphorbiaceae have been considered to be rather uniform (Webster, 1967; Cronquist, 1988). However, an interesting variation is seen in the pattern of integument initiation among various subfamilies. In angiosperms, the bitegmic ovules usually have their inner integument derived from the dermal layer and the outer chiefly from subdermal cells of the ovular primordium (Bouman, 1974). Bor & Bouman (1974) and Bor & Kapil (1975, 1976) noticed the unique occurrence of subdermal initiation of both inner and outer integuments in *Euphorbia milii* Des Moulins, *E. geniculata* Orteg. (Euphorbioideae), *Codiaeum variegatum* Blume (Crotonoideae), and *Crozophora obliqua* A. Juss. (Acalyphoideae). In *Bischofia javanica* Blume (Kapil & Bhatnagar, 1980) and *Securinega leucopyrus* (Willd.) Muell.-Arg. (unpublished obs.) both

of the integuments are initiated by divisions in dermal cells of the ovular primordium. Thus, the biovulate Phyllanthoideae differ prominently from the uniovulate subfamilies of the Euphorbiaceae. Corresponding details, yet unknown for the Oldfieldioideae, would be significant.

In the Phyllanthoideae, with dermal initiation of both integuments, the subdermal cells, too, contribute to the development of the core of the thickened base of the integuments, particularly of the outer one. Similarly, in the Acalyphoideae, Crotonoideae, and Euphorbioideae, which have subdermal initiation of the integuments, the epidermal layer of each integument divides to form the apical portions (rim) of the integuments. It is therefore quite likely that the dermal integuments of the Phyllanthoideae and subdermal integuments of the Acalyphoideae, Crotonoideae, and Euphorbioideae owe their origin to a common ancestral condition in which both dermal and subdermal cells contributed to the development of the integuments.

3. *Nucellar beak, nucellar cap, and obturator.* A majority (*Phyllanthus*, Mukherjee & Padhye, 1964; *Melanthesa*, R. P. Singh, 1968; *Sauropus*, *Breyenia*, P. N. Rao, 1970; *Securinaga*, unpublished obs.) of the Phyllanthoideae have a well developed nucellar beak that projects beyond the integuments and comes in contact with the obturator outside the micropyle. The beak is produced by divisions in both the parietal tissue and the dermal layer of the apical part of nucellus. Venkateswarlu et al. (1973) illustrated ovules with prominent nucellar beaks in *Meineckia parviflora* (Wight) Webster, *Chorisandra pinnata* Wight, and other Phyllanthoideae. In *Bischofia* the nucellus has an active micropylar axial tissue derived from the parietal cell. The epidermal layer also divides periclinally and anticlinally to contribute to the prominent nucellar cap, which does not extend beyond the micropyle. *Putranjiva roxburghii* Wall. (R. P. Singh, 1970a) is, however, an exception within the Phyllanthoideae in which the upper portion of the nucellus is reported to be insignificant and ephemeral. *Micranthemum* and *Picrodendron* of the Oldfieldioideae (Berg, 1975; fig. 29 in Hakki, 1985) also show a prominent nucellar cap derived by divisions in both the dermal and subdermal cells of the nucellus. The Acalyphoideae (*Micrococca*, Nair & Abraham, 1963; *Acalypha*, Banerji, 1949, Mukherjee, 1962; *Chrozophora*, Bor & Kapil, 1976) have a prominent nucellar beak derived from both dermal and subdermal cells. The beak extends far beyond the micropyle in *Chrozophora*. In *Dalechampia* (R. P. Singh & Pal, 1968; G. L.

Webster & B. D. Webster, 1972) and *Tragia* (Mukherjee, 1962) it grows up to the exostome, whereas in *Ricinus* (R. P. Singh, 1954), *Mallotus* (Thathachar, 1953a), *Micrococca*, and *Acalypha* it does not cross the endostome. The Crotonoideae (*Jatropha*, Mukherjee, 1962; *Codiaeum*, Bor & Bouman, 1974; *Baliospermum*, P. N. Rao, 1970), too, are characterized by the presence of a prominent nucellar beak. In the Euphorbioideae the extent of nucellar development shows far more variation. A large number of them (*Hura*, P. N. Rao, 1970; *Sapium*, Chopra, 1970; *Sebastiania*, Nair & Maitreyi, 1962) possess a well-developed nucellar cap that does not extend outside the micropyle. In *Euphorbia*, some species (e.g., *E. hypericifolia* L., Mukherjee, 1957; *E. helioscopia* L., R. P. Singh, 1969) have a long nucellar beak, whereas others (e.g., *E. geniculata*, Bor & Kapil, 1975; *E. milii*, Bor & Bouman, 1974; *E. peltata* Roxb., Mukherjee, 1965) have a short beak or a nucellar cap that does not extend beyond the micropyle.

Presence of a nucellar beak in the Euphorbiaceae is more widespread and seems to represent the primitive state of the character. The beak extends out of the micropyle and comes in contact with the obturator. Reduction in size of the nucellus (so that it is in the form of a cap which does not extend beyond the micropyle) is correlated with more extensive development of the obturator. In fact, in ovules with a projecting nucellar beak the obturator is small and its cells are compactly arranged. On the other hand, when the nucellus is smaller in extent, the obturator is prominent and its trichomelike epidermal cells project into the micropyle and come in contact with the nucellar tip. Both obturator and the nucellar beak/cap are supposed to be involved in the nutrition of the pollen tube as well as in guiding it to the embryo sac. Their correlated development is, therefore, complementary.

4. *Ontogeny of the female gametophyte.* The monosporic, 8-nucleate female gametophyte of the *Polygonum* type characterizes over 80 per cent of the investigated angiosperms (Maheshwari, 1950) and is therefore regarded as the primitive state. In the Euphorbiaceae, the Phyllanthoideae (*Phyllanthus*, *Putranjiva*, *Bischofia*) have the *Polygonum* type of female gametophyte. Information on female gametophytes is lacking in the Oldfieldioideae. In the Acalyphoideae, *Chrozophora*, *Micrococca*, and *Dalechampia* have the *Polygonum* type of female gametophyte, whereas *Acalypha* (Tateishi, 1927; Mukherjee, 1958; Johri & Kapil, 1953; Kapil,

1960) and *Mallotus* species (Ventura, 1934; Thathachar, 1953a) have tetrasporic embryo sacs of *Penaea*, *Acalypha indica*, *Peperomia hispidula*, or *Drusa* types. The Crotonoideae (*Codiaeum*, *Jatropha*), too, are reported to have only the *Polygonum* type of embryo sac. In the Euphorbioideae, *Sebastiania* and *Sapium* have the *Polygonum* type of embryo sac. However, the genus *Euphorbia* is unique. While a majority of its species (e.g., *E. geniculata*, *E. milii*, *E. heterophylla* L., and *E. pilosa* L.) have the *Polygonum* type of embryo sac, others show tetrasporic, *Fritillaria/Euphorbia dulcis* type (*E. dulcis*; Kapil, 1961; Battaglia, 1986) or *Penaea* type (*E. palustris* L.; Modilewski, 1911).

It thus seems obvious that a *Polygonum* type of embryo sac represents the primitive state in the Euphorbiaceae. From this, the tetrasporic type appears to have evolved independently in some Acalyphoideae and Euphorbioideae.

5. *Development of endosperm.* Irrespective of the number of nuclei participating in the formation of the primary endosperm nucleus, the basic pattern of development and behavior of endosperm is remarkably uniform in the Euphorbiaceae (see Kapil & Bhatnagar, 1972). The primary endosperm nucleus divides earlier than the zygote. Free nuclear divisions continue until 32–256 nuclei are produced. Wall formation is usually initiated at the globular or heart-shaped stages of the proembryo. It usually begins at the micropylar end and later extends along the periphery of the embryo toward the chalazal end (e.g., in *Ricinus*, *Aleurites*, *Hevea*, *Chrozophora*, *Micrococca*, *Sebastiania*, *Euphorbia*) or the wall may be laid down simultaneously along the periphery of the embryo sac (in *Acalypha*; Johri & Kapil, 1953). Wall formation extends centripetally until the entire endosperm becomes cellular. The first formed endosperm cells divide periclinally so that tiers of radially arranged cells are produced.

Of the large number of taxa investigated, only three species of *Croton*—*C. sparsiflorus* Morong (= *C. bonplandianum* Baill.), *C. klotzschianus* Gamble (Venkateswarlu & Rao, 1963), and *C. oblongifolius* Roxb. (Pal, 1972)—are known to form free nuclear chalazal endosperm haustorium. Initiated as a small protrusion at the 4- or 8-nucleate stage, it gradually develops into an elongate structure. Simultaneously, free nuclear divisions continue and the nuclei are dispersed peripherally with greater accumulation in the micropylar part. Cell formation is restricted to the micropylar part of the embryo sac, whereas the chalazal portion forms

a free nuclear caecumlike structure, which sometimes attains a length of 1000  $\mu\text{m}$  and behaves as an aggressive chalazal haustorium.

The presence of endosperm haustorium is a specialized feature that seems to have evolved only in the advanced Crotonoideae (*Croton* spp.).

6. *Caruncle.* In several Euphorbiaceae the apical part of the outer integument proliferates after fertilization to produce a soft and fleshy structure, the caruncle, around the micropyle. Its cells enlarge and may be parenchymatous (*Chrozophora*; Bor & Kapil, 1976) or their basal peripheral cells may develop into stone cells (*Micranthemum*; Berg, 1975). The caruncle has been regarded as useful in seed dispersal by ants (Berg, 1975), but its role in exerting stress for opening the locule, in the explosive dispersal of seeds (see Beer & Swaine, 1977), and in facilitating the process of seed germination by absorption of water, deserves further attention.

In the Phyllanthoideae, many of which are trees with drupaceous fruit, the seeds are mostly without a caruncle (*Phyllanthus*, *Putranjiva*, *Melanthesa*, *Sauropus*, *Bischofia*). In the Oldfieldioideae the seeds are described as "often carunculate" (Webster, 1987a). However, Berg (1975) described a well-developed caruncle in *Micranthemum*. In the Acalyphoideae a large majority (e.g., *Chrozophora*, *Acalypha*, *Ricinus*) have carunculate seeds, but a few such as *Dalechampia* lack a caruncle (Webster & Webster, 1972). Curiously, in *Acalypha indica* seeds of the lateral flowers in the inflorescence are carunculate, whereas the single seed of the terminal flower is ecarunculate (Johri & Kapil, 1953). In the Crotonoideae, too, the majority (e.g., *Jatropha*, *Codiaeum*, *Croton*) of investigated taxa have a caruncle. In the Euphorbioideae a caruncle is present in seeds of *Sebastiania* (Nair & Maitreyi, 1962), but is absent in *Excoecaria* (P. N. Rao, 1970) of the same tribe Hippomaneae. In *Euphorbia* some species have a well-developed caruncle (i.e., *E. dulcis*, Kapil, 1961), whereas others have an inconspicuous structure on the ventral micropylar side (*E. milii*, Bor & Bouman, 1974; *E. geniculata*, Bor & Kapil, 1975).

In the Phyllanthoideae the outer integument is dermal in origin and remains 2–4 cell layers thick. As observed in *Phyllanthus* spp. (Mukherjee & Padhye, 1964), *Melanthesa rhamnoides* Wight (R. P. Singh, 1968) and *Bischofia javanica* (Bhatnagar & Kapil, 1973; Bhatnagar, 1978) the tip of the outer integument does not proliferate so that the seed is ecarunculate. In *Micranthemum* of the

Oldfieldioideae the caruncle is produced primarily by divisions of the inner dermal layer at the apical region of the outer integument (Berg, 1975). In Acalyphoideae, Crotonoideae, and Euphorbioideae the outer integument is subdermal in origin (Bor & Bouman, 1974; Bor & Kapil, 1976). The caruncle is formed by proliferation of both subdermal and dermal apical cells of the outer integument. Interestingly, in *Euphorbia geniculata* (Bor & Kapil, 1975) an inconspicuous caruncle develops around the micropyle, on the ventral side of the young seed, by divisions of the dermal cells. In some other species of *Euphorbia* that lack a caruncle, the tip of the outer integument nevertheless shows some proliferation of cells (*Euphorbia milii*; Bor & Bouman, 1974).

It seems, therefore, that formation of a caruncle is a derived feature in the Euphorbiaceae, and its absence in some Euphorbioideae represents the result of secondary loss of this feature.

#### CIRCUMSCRIPTION OF THE EUPHORBIALES

According to Webster (1987a), "Over 30 families have been included in the Euphorbiales by leading botanists in the 19th and 20th centuries." Of these, the inclusion of the Empetraceae, Stackhousiaceae, Fouquieriaceae, Batidaceae, Gyrosteromonaceae, and Nepanthaceae appears to be far-fetched. In fact, several taxa, often with simple, unisexual flowers, tricarpeal ovary with one or two ovules in each locule, carunculate seed, and explosive mechanism of seed dispersal were earlier assigned to the Euphorbiaceae or placed close to them. This led to the family acquiring the reputation of a "dust-bin" group. More critical investigations revealed that the resemblance was quite often a result of convergence on account of adaptation to a similar mode of pollination and seed dispersal. Embryological studies, together with evidence from other disciplines such as palynology (Punt, 1962; Köhler, 1965), floral anatomy (V. Singh & Asha Singh, 1975), and wood anatomy (Hayden, 1977; Mennega, 1987) helped in the removal of many alien taxa from the Euphorbiaceae. Only such examples which can possibly have some affinities, and where embryological characters have helped in the circumscription of the family as a more natural group, are considered here.

#### 1. BUXACEAE

The boxwoods, because of their simple flowers, tricarpeal ovary, axile placentation, presence of one or two anatropous, bitegmic, and crassinucellate ovules in each locule, and seeds that are some-

times carunculate, were, and still are, often referred close to the Euphorbiaceae (Stebbins, 1974; Bensen, 1979; Cronquist, 1981; Rouleau, 1981). There are some other similarities too; for example, in *Buxus* L. an obturator is present and the ovule has a nucellar cap formed by periclinal divisions in the nucellar epidermis. However, the Buxaceae show many-layered anther tapetum, ovules with a dorsal raphe, dermal inner and subdermal outer integument (see fig. 3D in Wiger, 1935), persistent antipodal cells which even multiply, and fusion of polar nuclei at the chalazal part of the central cell. More important differences lie in the development of endosperm, which is cellular, and seeds, which are exo-mesotestal (Wiger, 1935; Corner, 1976). A report of nuclear endosperm in *Sarcococca* Lindl. needs confirmation. There is thus little justification even for the grouping together of the Buxaceae and the Euphorbiaceae in the same order.

#### 2. DAPHNIPHYLLACEAE

While most taxonomists now agree that *Daphniphyllum* Blume should be placed in a separate family, disagreement still exists with regard to its affiliations. Emberger (1960), Stebbins (1974), and Rouleau (1981) prefer it to be a part of the Euphorbiales, but Hutchinson (1973), Takhtajan (1980, 1983, 1987), Cronquist (1981), and Goldberg (1986) consider it closer to the Hamamelidales.

Our palynological and embryological investigations of *Daphniphyllum himalayense* Muell. Arg. (Bhatnagar & Garg, 1977; Bhatnagar & Kapil, 1982) assign it a distinctive position from the Euphorbiaceae. This is because it has 3-traced stamens, 8-10 anther wall layers, thickened radial and inner tangential walls of the endothelial cells (without fibrous thickenings), a 2- or 3-layered tapetum, a bicarpeal ovary with two to four parietal ovules, and subdermal outer and dermal inner integument. Moreover, an obturator is absent, the endosperm is cellular, the embryo is small, the seeds have perisperm and are endotegmic and ecarunculate.

*Daphniphyllum* resembles the Hamamelidales (see Kapil & Kaul, 1972; Kaul & Kapil, 1974) in having an 8-layered anther wall, a bicarpeal, bilocular ovary with incomplete partition, two ovules in each locule, parietal placentation, anatropous, bitegmic, crassinucellate ovules with subdermal outer and dermal inner integument, absence of an obturator, persistent antipodals, cellular endosperm and polyembryony. Nevertheless, it is different from the Hamamelidaceae in having 3-traced stamens



and an endotegmic seed coat. Thus, its inclusion in an independent family Daphniphyllaceae, within the order Hamamelidales or in an independent order Daphniphyllales close to it, appears more satisfactory.

### 3. SIMMONDSIACEAE

Although there is consensus that *Simmondsia* Nutt. should form an independent family, the Simmondsiaceae, its phylogenetic relationship is still debated. Cronquist (1981, 1988), Thorne (1983), and Dahlgren (1983) place it in the Euphorbiales, whereas others relate it to the Buxaceae (Emberger, 1960), Hamamelidales (Takhtajan, 1983), or the Fagales (Goldberg, 1986).

*Simmondsia* shares a few embryological traits with the Euphorbiaceae—both have anatropous, bitegmic, crassinucellate ovules and nuclear endosperm. However, it differs from the spurges in having ovules with a dorsal raphe, absence of an obturator and hypostase and in its possessing exomesotestal, exalbuminous seeds. There is no doubt that the Simmondsiaceae are not related to the Euphorbiales, and are perhaps quite out of place in the Buxales or the Hamamelidales as well. Goldberg's (1986) suggestion that *Simmondsia* is related to the Fagales deserves consideration. The presence in both of a 3- to 5-layered anther wall, a nucellar cap, nuclear endosperm, a large vacuole in the chalazal part of the endosperm (see Wiger, 1935; Davis, 1966), exalbuminous, exotestal seeds, and a large, straight embryo with thick cotyledons (Corner, 1976) is indicative of such a relationship.

### 4. BISCHOFIA

*Bischofia javanica*, a tall deciduous tree, has been placed either in the tribe Phyllanthae or in an independent tribe Bischofeae within the subfamily Phyllanthoideae (Hutchinson, 1969; Webster, 1987a). However, Airy Shaw (1965, 1966) assigned the same genus to an independent family, Bischofiaceae, which he thought was related to the Staphyleaceae.

An embryological study of *Bischofia javanica* (Bhatnagar & Kapil, 1973, 1979; Bhatnagar, 1978) indicated that this species resembles other Phyllanthoideae (Mukherjee & Padhye, 1964; Chopra & Singh, 1969; R. P. Singh, 1970a) even in minute details. The common features are: a 5-layered anther wall, fibrous endothecium, ephemeral middle layers, a secretory tapetum with multinucleate cells, a tricarpeal ovary, two anatropous, bitegmic, crassinucellate ovules with a ventral raphe borne on axile placenta in each locule,

dermal integuments (as in *Securinega*), formation of a nucellar cap and placental obturator, differentiation of hypostase, a *Polygonum* type of embryo sac, Onagrad embryogeny, and exotegmic seeds. Hence, the removal of *Bischofia* from the Euphorbiaceae is uncalled for.

### 5. PICRODENDRON

This genus has been variously classified in the Anacardiaceae, Bombacaceae, Burseraceae, Euphorbiaceae, Juglandaceae, Sapindaceae, and Simaroubaceae (see Hakki, 1985). Webster (1987a) treated it as a tribe Picrodendreae in the subfamily Oldfieldioideae of the Euphorbiaceae.

Hakki (1985) studied some aspects of floral morphology and embryology of the West Indies species *Picrodendron baccatum* (L.) Krug & Urban. It certainly resembles the Euphorbiaceae in having two collateral, anatropous, bitegmic and crassinucellate ovules borne on axile placenta, and presence of a nucellar cap, obturator, and hypostase. Based on morphological and palynological features, Hayden et al. (1984) strongly supported an alliance of *Picrodendron* with the Oldfieldioideae. *Picrodendron* is distinct in having a bicarpellary, bilocular ovary and embryo with folded cotyledons. An investigation of the anther, female gametophyte, endosperm, and seed of *Picrodendron* and the Oldfieldioideae would be of considerable interest from a taxonomic viewpoint.

### 6. CALLITRICHACEAE

The euphorbiacean connection of the Callitrichaceae is indeed quite discredited (Webster, 1987a). The unitegmic, tenuinucellate ovules, differentiation of endothelium, cellular endosperm with terminal haustoria, long filamentous proembryonal suspensor, and minute seeds with membranous seed coats (Netolitzky, 1926; Maheshwari, 1963) are a far cry from the Euphorbiaceae. On the basis of their embryology and seed structure the Callitrichaceae are far more comfortable in or near the Lamiales (Stebbins, 1974; Takhtajan, 1980; Thorne, 1983; Dahlgren, 1983).

### 7. AEXTOXICACEAE

A monotypic family endemic to Chile, the Aextoxicaceae have been assigned to the Euphorbiales by Stebbins (1974), Takhtajan (1983), Thorne (1983), and Goldberg (1986); Hutchinson (1973), Cronquist (1981), Rouleau (1981), and Webster (1987a) prefer it to be in the Celastrales. This taxon is embryologically not well understood. It has

anatropous, bitegmic, crassinucellate ovules with massive nucellar beaks (Mauritzon, 1936). However, its bicarpellary, unilocular ovary with one bifid style and two subapical ovules (Goldberg, 1986), endostome extending considerably beyond the exostome, embryo extending only up to half the length of the endosperm, and ruminant endosperm give the impression that it may not be related to the Euphorbiaceae.

#### 8. DICHAPETALACEAE

The Dichapetalaceae, a small family of four genera centered in Africa, have been included in the Euphorbiales (Emberger, 1960; Rouleau, 1981; Takhtajan, 1983; Thorne, 1983; Dahlgren, 1983), Rosales (Hutchinson, 1973), Thymelaeales (Melchior, 1964), and the Celastrales (Cronquist, 1981; Goldberg, 1986). Punt (1975) did not observe any significant resemblance of its pollen with that of the Euphorbiaceae and suggested its greater similarity with the Malpighiaceae. From what is known about its embryology, it seems that it has a bi- or tricarpellary ovary, two ovules in each locule on axile placentation, and carunculate seeds like those of the Euphorbiaceae. However, its unitegmic ovules (Corner, 1976) and exalbuminous seeds do not accord well with the Euphorbiaceae. Its resemblance is rather far more with the Icacinaceae (see Davis, 1966) and other Celastrales (Goldberg, 1986).

#### 9. THYMELAEACEAE

The Thymelaeaceae have been placed in the Myrtales (Stebbins, 1974; Benson, 1979; Cronquist, 1981) and the Euphorbiales (Thorne, 1983). Takhtajan (1980) and Dahlgren (1983) raised them to an independent order, the Thymelaeales, which is juxtaposed to the Euphorbiales in the superorder Malviflorae.

Erdtman (1952) emphasized the resemblance in the "crotonoid" exine pattern of some Euphorbiaceae and Thymelaeaceae. Wunderlich (1967) and Corner (1976) pointed out that both these taxa are characterized by exotegmic seeds. Other common embryological features are: tetrasporangiate anther, fibrous endothecium, ephemeral middle layers, secretory tapetum, axile placentation, anatropous or hemianatropous, bitegmic crassinucellate ovules, presence of nucellar beak and hypostase, often carunculate seeds, and straight embryo extending all along the seed (see Davis, 1966; Corner, 1976). However, unlike Euphorbiaceae, the Thymelaeaceae have a stylar obturator and persistent and multiplicative antipodal cells, and the endo-

sperm is usually scanty or absent. It is therefore better to assign the Thymelaeaceae to a separate order, the Thymelaeales, next to the Euphorbiales in the superorder Malviflorae. The alternative view of the alliance of the Thymelaeaceae with the Myrtales is much less convincing. The Myrtaceae have numerous ovules in the ovary, lack an obturator and hypostase, are frequently polyembryonous (Netolitzky, 1926; Corner, 1976) and have seeds that are ecarunculate, with a testal seed coat.

#### 10. PANDACEAE

Pandaceae, another small family with four genera, is distributed mostly in western Africa and southeastern Asia. With their bilocular anthers, orthotropous ovules (in *Panda* Pierre), lack of obturator, and fruits dehiscing by valves (Goldberg, 1986), they no doubt deserve to be segregated from the Euphorbiaceae in an independent family, the Pandaceae. Whether this family should be placed in the Euphorbiales (Cronquist, 1981, 1988; Takhtajan, 1983, 1987; Thorne, 1983; Goldberg, 1986; Radcliffe-Smith, 1987) or allied to the Celastrales (Melchior, 1964; Hutchinson, 1973) cannot be stated unequivocally until more embryological data become available on the Pandaceae.

#### AFFINITIES OF THE EUPHORBIALES

The Euphorbiales have been considered by different authors to be affiliated with one of the two subclasses, the Dilleniidae (Violales and Malvales) or the Rosidae (Celastrales and Geraniales). Suggestions with regard to the relationships of the Euphorbiales have been mostly confined to these four orders:

1. Celastrales (Stebbins, 1974; Cronquist, 1981, 1988);
2. Geraniales (Melchior, 1964; Webster, 1987a);
3. Violales (Hickey & Wolfe, 1975);
4. Malvales (Croizat, 1973; Takhtajan, 1980, 1987; Dahlgren, 1983; Thorne, 1983; Goldberg, 1986).

The Celastrales (which may include Aquifoliaceae, Stackhausiaceae, Icacinaceae, Siphonodontaceae, Sphenostemonaceae, and Goupiaceae, for purposes of the present comparison) are mostly trees and shrubs with bisexual flowers, tetrasporangiate anthers, 5- or 6-layered anther walls, fibrous endothecium, ephemeral middle layers, a secretory tapetum, a superior, semi-inferior or inferior ovary, two to five carpels, one to five (Celastraceae) or up to ten locules (Siphonodontaceae), mostly one or two ovules per locule (two to six in Siphono-

dontaceae and up to 18 per locule in Celastraceae), axile placentation, anatropous, bitegmic or unitegmic, crassinucellate or tenuinucellate ovules, a dorsal raphe in ovules with upwardly directed micropyle or ventral in ovules with downwardly directed micropyle, presence of endothelium, a *Polygonum* type of embryo sac, ephemeral antipodals, Solanad or Caryophyllad type of embryogeny, multiplicative testa with outer epidermis developing into a palisadelike layer, tegmen with outer epidermis forming thick-walled fibers, and capsular fruit (sometimes a drupe or berry).

The Celastrales differ from the Euphorbiales in having bisexual flowers, unitegmic, tenuinucellate ovules (in Aquifoliaceae), a dorsal raphe in ovules with micropyle facing upward, single-celled archesporium, 8–15 antipodal cells (in Stackhousiaceae), cellular endosperm (in Aquifoliaceae and Icacinaceae) with chalazal haustorium (Swamy & Ganapathy, 1957), Caryophyllad or Solanad type of embryogeny, embryo mostly small, and outer epidermis of outer integument forming a palisadelike layer. There are significant similarities, too, in the structure of anther, ovule, and in fibrous thickenings in the outer epidermis of the inner integument. The differences, however, far outweigh the similarities.

The Geraniales (including Geraniaceae, Oxalidaceae, Limnanthaceae, Tropaeolaceae, Vivianiaceae, and Balsaminaceae) are a cosmopolitan group, usually with herbs and shrubs. Their other characteristics are: bisexual flowers, 4- or 5-layered anther wall with secretory or amoeboid tapetum, three to five carpels, one, two, or several ovules per locule, axile placentation, anatropous, campylotropous or amphitropous, bitegmic, crassinucellate (Geraniaceae), unitegmic, tenuinucellate (Limnanthaceae) or bitegmic, tenuinucellate (Oxalidaceae) ovules. Endothelium, obturator, and hypostase are present. The female gametophyte is of the *Polygonum* type, the endosperm is nuclear or helobial, copious or absent, the embryo has haustorial proembryonal suspensor (Tropaeolaceae), and the embryogeny is of Solanad type. Seeds are sometimes arillate, and the exotegmen forms a mechanical layer with an undulated outline (Geraniaceae). The exotegmen is fibrous in Oxalidaceae, and seeds are unitegmic, pachychalazal in Balsaminaceae and Limnanthaceae (Davis, 1966; Johri, 1970; Narayana, 1970a–c; Corner, 1976).

The Geraniales exhibit considerable diversity among themselves. They differ from the Euphorbiales in many features, e.g., in the presence of amoeboid tapetum, several ovules in each locule, unitegmic and tenuinucellate ovules, endothelium,

endosperm haustorium (in Limnanthaceae) and suspensor haustorium (in Tropaeolaceae), Solanad type of embryogeny, and artillate seeds. Although there is some resemblance in the fibrous or palisadelike exotegmen of the Oxalidaceae and Geraniaceae with the Euphorbiales, the behavior of the outer integument is quite different. The Geraniales are, therefore, unlikely to be close relatives of the Euphorbiales.

The Violaes are a pantropical and subtropical group incorporating families such as the Flacourtiaceae, Passifloraceae, Caricaceae, Turneraceae, Violaceae, and Cucurbitaceae. They have tetrasporangiate anthers, a 5-layered anther wall, fibrous endothecium, secretory tapetum, three to five carpels, superior-inferior, usually monolocular ovary, mostly numerous ovules in each locule, parietal, rarely axile or apical placentation, anatropous, hemianatropous or orthotropous, bitegmic, crassinucellate ovules with nucellar cap, hypostase consisting of a pocket of cutinized cells (podium), tannin-containing postament and sclerotic chalazal part, *Polygonum* type of embryo sac, nuclear endosperm (often scanty or absent in seed), Asterad type of embryogeny, straight embryo with thin cotyledons, usually numerous seeds with aril arising from raphe, fibrous exotegmen, and fruit mostly a berry (Davis, 1966; D. Singh, 1970a–d; Kaur, 1970; Corner, 1976).

The Violaes resemble the Euphorbiales in their structure of anther, ovule, and seed. However, certain characteristics of the violaceous families, such as their monolocular ovary, numerous ovules, parietal placentation, absence of obturator, persistent pollen tubes, Asterad type of embryogeny, aril arising from the raphe, and reduction or absence of endosperm, give the impression that they are widely separated from the Euphorbiaceae.

The Malvales, a cosmopolitan group of herbs, shrubs, and trees, predominantly distributed in the subtropical areas, include the Sterculiaceae, Elaeocarpaceae, Tiliaceae, Malvaceae, Dipterocarpaceae, and Bombacaceae. They have mostly bisexual flowers, bisporangiate or tetrasporangiate anthers, 4- or 5-layered anther wall, fibrous endothecium, ephemeral middle layers, secretory tapetum with multinucleate cells, polysiphonous pollen, usually five carpels, one to many ovules per locule, axile (rarely parietal) placentation, anatropous, hemianatropous or campylotropous, bitegmic, crassinucellate ovules, differentiated hypostase, multicellular archesporium, *Polygonum* type of embryo sac, ephemeral antipodal cells (rarely multiplicative), nuclear endosperm, sometimes with chalazal haustorium (Bombacaceae), Asterad

or Onagrad type of embryogeny, straight, curved or folded embryo, extending all along the length of the endosperm, winged, hairy or arillate seeds with exotegmen forming a palisadelike layer of sclerotic (Malpighian) cells, and capsule or schizocarpic fruit (Davis, 1966; Corner, 1976). Thus, the Malvales show abundant similarity with the Euphorbiales in the structure of the anther, ovule, embryo sac, endosperm, embryo, and seed, and are undoubtedly nearer to the Euphorbiales.

The relationship of the Euphorbiales with the major groups of dicotyledons is difficult to decide without some element of ambiguity because the groups in question are themselves rather ill-defined. Various taxonomists, such as Dahlgren (1975), Cronquist (1981, 1988), Thorne (1983), Takhtajan (1987), and Goldberg (1986) have composed their Celastrales, Geraniales, Violales, and Malvales in different ways and have placed them at varying distances from the Euphorbiales and from each other. Many of their smaller families are little known embryologically. At the present level of understanding, the Euphorbiales are undoubtedly closer to the Malvales than to the other three orders discussed here. In view of this, inclusion of the spurges among the Dilleniidae is justified on embryological grounds.

#### CLASSIFICATION OF THE EUPHORBIACEAE

The subfamilies of the Euphorbiaceae as circumscribed by Webster (1975, 1987a) can be characterized embryologically as follows:

**SUBFAMILY 1. PHYLLANTHOIDEAE:** 2-nucleate pollen grains with nonspinulose exine, two ovules per locule, dermal initiation of both integuments, well-developed nucellar beak, *Polygonum* type of embryo sac, broad cotyledons, ecarunculate seeds with fibrous exotegmen.

**SUBFAMILY 2. OLDFIELDIOIDEAE:** 2-nucleate pollen with usually spinulose exine, two ovules per locule, presence of nucellar cap, narrow cotyledons, often carunculate seeds (caruncle derived from inner epidermis of outer integument) with fibrous exotegmen.

**SUBFAMILY 3. ACALYPHOIDEAE:** 2-nucleate pollen, nonspinulose and noncrotonoid exine, one ovule per locule, subdermal initiation of both integuments, well-developed nucellar beak, monosporic or tetrasporic embryo sac (*Acalypha* and *Mallo-tus*), and carunculate seeds (caruncle derived from dermal as well as subdermal cells of outer integument) with palisadelike exotegmen.

**SUBFAMILY 4. CROTONOIDEAE:** 2- or 3-nucleate pollen mostly with "Croton" type of exine, one ovule per locule, subdermal initiation of both integuments, well-developed nucellar beak, presence of endosperm haustoria (in *Croton*) and hypocotyledonary seminal roots, mostly carunculate seeds with palisadelike exotegmen.

**SUBFAMILY 5. EUPHORBIOIDEAE:** 2- or 3-nucleate pollen with reticulate or tectate exine, one ovule per locule, subdermal initiation of both integuments, presence of nucellar beak or cap, monosporic or tetrasporic embryo sac (*Euphorbia* spp.), carunculate or ecarunculate seeds with palisadelike exotegmen.

On the basis of the distribution of the above-mentioned features, there is no doubt that the subfamilies and tribes of Euphorbiaceae share a large number of correlated characters. Even when they differ, usually a perceptible pattern of evolution is recognizable. As indicated by Webster & Rupert (1973) there is a definite trend of evolution of 3-nucleate pollen from a 2-nucleate condition within the Crotonoideae and Euphorbioideae. A nucellar beak is present in all the groups but there is a trend of reduction in the Phyllanthoideae, Oldfieldioideae, and Euphorbioideae. In *Euphorbia* some species have a nucellar beak, whereas others have only a cap. The female gametophyte is of the *Polygonum* type and only in Acalyphoideae and Euphorbioideae is there a localized derivation of tetrasporic embryo sac. Endosperm development is remarkably uniform, with initial free nuclear divisions and subsequent centripetal wall formation. *Croton* spp. are exceptional in having endosperm haustoria as well. The seeds are exotegmic and have developed a caruncle in correlation with the explosive mechanism of seed dispersal. In the Euphorbioideae, even when the caruncle is absent, the apical part of the outer integument proliferates to some extent, indicating a secondary loss. It is thus apparent that behind the façade of diversity, the Euphorbiaceae are in fact a homogeneous group that could have evolved on a monophyletic basis from an as yet unknown group within the Dilleniidae.

It is likely that the evolutionary line that gave rise to the Acalyphoideae, Crotonoideae, and Euphorbioideae split rather early from the line that produced the Phyllanthoideae (and Oldfieldioideae). This is inferred because the biovulate condition, the dermal initiation of both integuments, and the fibrous exotegmen in the Phyllanthoideae (and Oldfieldioideae?) are fundamentally different from the uniovulate condition, the subdermal initiation of

both integuments, and the palisadelike exotegmen of the Acalyphoideae, Crotonoideae, and Euphorbioideae. Moreover, in the Oldfieldioideae the caruncle is reported to have a dermal origin (*Micranthemum*; Berg, 1975), whereas in the Acalyphoideae it is formed by the proliferation of both dermal and subdermal cells (*Chrozophora*; Bor & Kapil, 1976). In the Crotonoideae, too (*Codiaeum*; Bor & Bouman, 1974), the caruncle is constituted by the cells derived from dermal tissue of the outer integument. The Crotonoideae and Euphorbioideae seem to have evolved as independent lines from the Acalyphoideae (cf., Webster, 1987b).

Thus, the pattern of distribution of embryological characters in different subfamilies gives an impression that the evolution within the Euphorbiaceae has progressed as follows: (i) From an early ancestral condition one phyletic line gave rise to the Phyllanthoideae and the Oldfieldioideae; (ii) a second line gave rise to the Acalyphoideae from which the Crotonoideae and the Euphorbioideae evolved as separate lines.

Corner (1976) proposed a cleavage in the Euphorbiaceae on the basis of the fact that the Phyllanthoideae have fibrous exotegmen, whereas the Crotonoideae possess exotegmen with palisade (Malpighian) cells. According to him the palisadelike exotegmen of the Crotonoideae aligned them with the Bombacaceae–Malvaceae–Sterculiaceae–Tiliaceae. On the other hand, the fibrous exotegmen of the Phyllanthoideae made them look closer to the Celastraceae–Flacourtiaceae–Violaceae. In our opinion, the differences in seed structures do not indicate a diphyletic origin of the Euphorbiaceae, particularly because various intermediates are seen in the Euphorbiaceae family itself. For example, in *Bischofia* the exotegmen in the chalazal and micropylar parts is made up of palisadelike cells, whereas in the median regions it has fibers with ribbonlike thickenings.

Embryological data support the division of the family Euphorbiaceae into five subfamilies, as postulated by Webster (1975, 1987a). Since only 16 out of 50 tribes of the Euphorbiaceae are explored embryologically, it would be rather premature to give an opinion on tribal classification. Such an evaluation must await further work on the biology of reproduction of quite a large number of taxa.

#### CONCLUSIONS

A general survey of the embryological literature on the Euphorbiaceae gives an impression that it is an extensively investigated taxon. However, a

critical appraisal leads us to conclude that our information is confined to only about 30 genera belonging to 16 tribes out of 300 genera and 50 tribes recognized by Webster. In spite of this lacuna, it is not preposterous to list out the embryological features that uniformly characterize this family. The Euphorbiaceae display a remarkable homogeneity in the structure and development of anther, microsporogenesis, placentation, ovule, endosperm, embryo, and seed. Variation in pollen nuclear number, integument initiation, extent of nucellar growth, development of the female gametophyte and caruncle seems to represent an understandable pattern of evolution.

Embryological evidence supports the treatment of the Euphorbiaceae as a monophyletic group. Among its suspected allies, the Dichapetalaceae, Aextoxicaceae, and Pandaceae are poorly studied, and what is known about them does not justify their inclusion in the Euphorbiales along with the Euphorbiaceae. Buxaceae, Callitrichaceae, Daphniphyllaceae, and Simmondsiaceae are better known embryologically but have hardly anything in common with the Euphorbiaceae. *Bischofia* and *Picrodendron* certainly deserve to be retained in the Euphorbiaceae on embryological grounds. The Euphorbiales appear to be closer to the Malvales and the Thymelaeales rather than to other orders, as has often been advocated by systematists.

On the basis of distribution of embryological characters, Webster's classification of Euphorbiaceae into five subfamilies is supported. It appears that the uniovulate Acalyphoideae separated rather early from the biovulate Phyllanthoideae (and Oldfieldioideae), the most primitive spurges. The Crotonoideae and the Euphorbioideae probably arose from the Acalyphoideae as distinct lines. Present limitations of embryological data prevent any comments on the tribal classification of this interesting group of plants.

Research on the embryology of the Euphorbiaceae holds considerable promise for further elucidation of the affinities and classification of this large family. Studies on some of the little known tribes, for example, those of the Oldfieldioideae, and interpretation of the data, together with information from other disciplines, would go a long way toward understanding the saga of the spurges.

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